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Effects of Peanut Genotypes on *Meloidogyne* Species Interactions[1]

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Abstract: A 3-year microplot study was conducted to characterize the interaction between *Meloidogyne arenaria* race 1 (MA1) and *M. hapla* (MH), as affected by the five peanut genotypes: Florigiant, NC 7, NC 6, NC Ac 18416, and NC Ac 18016. The interactive effects on infection (total parasitic forms per root unit) and reproduction potentials of each nematode species and crop damage were determined. As a single population, MA1 had greater infection capacity and caused more crop damage than did MH, but both species had similar reproduction potentials. In mixed infestations, MA1 was more competitive than MH, as reflected by incidence of infection. Infection and reproduction potentials, and crop-damage capabilities of the mixed populations were similar to those of MA1 alone. All peanut genotypes were susceptible to infection by both nematodes. NC 6 was less susceptible to damage by MA1 and the mixed populations than other genotypes. A nematode treatment × genotype interaction was detected for root infection and crop damage, but not for population density or reproduction. With high preplant nematode levels (Pi), the populations reached their peak by midseason, whereas those with low Pi peaked after midseason. Crop damage in the second and third years was correlated with Pi level.

Key words: Arachis hypogaea, competition, infection potential, interaction, *Meloidogyne arenaria, M. hapla,* mixed population, parasitic fitness, peanut, reproduction potential, root-knot nematode.

Numerous nematode species can damage peanut (*Arachis hypogaea* L.) (16). In the United States, *Meloidogyne arenaria* (Neal) Chitwood is the most damaging species on peanut in the more southern states, and *M. hapla* Chitwood is the most damaging nematode in North Carolina, Virginia, and Oklahoma (1). Despite their relative importance, no peanut cultivar resistant or tolerant to these two nematode species is available (17,23).

Plant resistance to nematodes is generally characterized by restricted reproduction of the target nematode species (3). However, for nematodes that induce unique symptoms or damage such as root-knot species, resistance indices may be based jointly on restricted reproduction (host efficiency) and damage (root galling) (20). The expression of host resistance to a single nematode species could be affected by multispecies infections because parasitism by one species usually alters root physiology and thereby may affect suitability for other species (5). Resistance-breaking effects induced by concomitant feeding of endoparasitic nematodes have been documented on tobacco (5) and cowpea (13). Conversely, the related effects on plant growth or damage caused by a nematode species, acting either alone or in combination with others, could influence the host status of a plant, and, therefore, is an important factor in population dynamics of the parasite (19). Niblack et al. (18) demonstrated in microplot experiments that soybean genotypes did not affect the soil population densities of *M. incognita* (MI) second-stage juveniles (J2) in the presence of *Heterodera glycines* (HG), whereas those of HG J2 on susceptible cultivars were suppressed in the presence of MI.

Although concomitant infestations of *M. arenaria* race 1 and *M. hapla* are common in peanut fields in North Carolina, information on their possible interactions is limited (4,22). Because several peanut cultivars are planted, elucidation of their differential effects on an interaction between these two nematode species and consequent population dynamics, as well as crop damage,

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should be helpful in managing these pathogens.

The objectives of this study were i) to characterize the interaction between MA1 and MH, as affected by moderately resistant and susceptible peanut genotypes, and ii) to determine the effects of interactions on infection competition, reproduction potential, and parasitic fitness of each species on different peanut genotypes, and subsequent damage to crops.

Materials and Methods

Nematode infestation and plant culture: This study was conducted in microplots (4) for 3 years, using a split-plot experimental design consisting of nematode treatment as the main plot and peanut genotype as the subplot with six replications. Five nematode treatments included single populations of *M. arenaria* race 1 (MA1) and *M. hapla* (MH), half-inoculum-rate-mixture and full-inoculum-rate-mixture populations of the two nematode species, and noninoculated controls. The five peanut genotypes evaluated included two breeding lines, NC Ac 18416 and NC Ac 18016, previously reported to be more susceptible to MA1 than to MH (4); and three cultivars: 'Florigiant' (hypersusceptible to MA1, resistant to MH), 'NC 7' (resistant to MA1, hypersusceptible to MH), and 'NC 6' (resistant to MA1 and MH). The degree-of-resistance designation of the three cultivars was based on a report from greenhouse evaluations (21).

Two months before planting, field microplots (circular, 76-cm-d) established in Norfolk loamy sand (81% sand, 13% clay, 6% silt) at Central Crop Research Station, Clayton, North Carolina, were fumigated with methyl bromide/chloropicrin (98:2 w/w) (869 kg/ha). At planting date of the first year (year 1A, 1990), commercial preparation of *Bradyrhizobium* (cowpea type, Nitragin Co., Milwaukee, WI) was added to all microplots (5.6 kg/ha).

Nematode populations of MA1, originally from a peanut field in North Carolina, and MH, originally from tobacco-peanut rotation plots, also in North Carolina, were increased separately on tomato (*Lycopersicon esculentum* Mill. 'Rutgers') in a greenhouse. Eggs of the nematodes were extracted from roots with NaOCl (11). The initial inoculum concentrations (Pi) were 500 eggs/500-cm^3 soil of each nematode species for single population and full-inoculum-rate-mixture population treatments, and 250 eggs/500-cm^3 soil of each species for the half-inoculum-rate-mixture treatment. Nematode eggs suspended in water were introduced into appropriate plots by sprinkling 1,000 ml of the egg suspension on the soil surface. Inoculum was incorporated uniformly throughout the upper 15 cm soil. Control plots received a similar amount of water.

Twelve seeds of each genotype were planted per plot and plants were thinned to six plants after emergence. Irrigation was provided as needed. At flowering, each plot received one application of land plaster (22% Ca; 17% S [300 kg/ha]) as a calcium source. Leafspot control with chlorothalonil was applied as necessary.

In the second and third years, the carryover *Meloidogyne* populations from the previous year were tested against the same peanut genotypes. Plots were not reinfested with either Bradyrhizobium or nematodes. Before planting, microplots received fertilizer treatments based on a North Carolina Department of Agriculture soil test recommendation. Planting and cultural practices were as described for the first year.

In 1992, the first-year experiment was repeated (year 1B) with five replications in rectangular microplots (100 cm × 80 cm) with a Fuquay sand (91% sand, 3% clay, 6% silt; 0.6% OM) located at the same research station. Microplots were fumigated in the fall with methyl bromide/chloropicrin as previously described. Potassium fertilizer was added (based on soil test) before planting. At the time of nematode infestation, all microplots also received approximately 1,200 chlamydospores/plot of the endomycorrhizal fungus *Glomus macrocarpus* Tul. & Tul to promote plant

growth. Fifteen seeds were planted in the center row, and two seeds were planted in each side row. After emergence, seedlings were thinned to eight plants in the center row for harvest data, and one plant was left in either side row for midseason destructive root sampling. Application of a commercial preparation of *Bradyrhizobium* was made at 2 days after seeding and was repeated after 6 weeks due to poor nodulation. After 2 months, plants were fertilized once with Peter's 20-20-20 (N-P-K) (W.R. Grace & Co., Fogelsville, PA). Land plaster and general care of plants were provided as previously described in this study.

Nematode and crop assays: To determine the nematode population densities, soil samplings were made at midseason, about 100 days after planting, and at harvest, about 150 days after planting of each year, in early spring during the last week of February and at preplant, during the second week of May of the second and third years. Each soil sample consisted of 12 cores, 2.5-cm-d × 20-cm deep. A 500-cm^3 soil subsample was processed by elutriation and centrifugation to extract juveniles (2). Root fragments collected from the elutriator were used to extract eggs using NaOCl (2). Reproduction factors were calculated from nematode population densities in soil (J2 + eggs) at harvest (Pf)/initial inoculum or population densities at preplanting (Pi). Winter survival ratios of nematodes were computed from Pi of current year/Pf of immediate preceding year.

Subsamples of 250-cm^3 soil from midseason and harvest samplings were used for bioassays on MH-resistant watermelon 'Charleston Gray' in a greenhouse to characterize nematode interactions in the mixed populations. The bioassay soil was placed over 100 cm^3 of sterilized sand:soil mixture (1:1) in a 10-cm-d clay pot. A single 1-week-old watermelon seedling was transplanted into the pot and the soil was covered with 50 cm^3 of the sand:soil mixture. The pot was placed in an empty 15-cm-d clay pot to prevent contamination among adjacent plants. All pots were elevated above the greenhouse bench surface on inverted drainage saucers, and plants were maintained for 6 weeks. Root systems were washed free from soil and rated for root galling (0–100% area of galled roots per root system).

Root samplings from nematode-infested plots only were made at midseason and at harvest of the first year to determine the nematode population density, reproduction, and species proportion for the mixtures. The species-proportion determination was also made at harvest of the second year. Soil around the root zone was carefully dug with a trowel to collect about 3 g roots. However, root sampling in the rectangular microplots for the repeated first-year study, year 1B in 1992, was done only at midseason by digging up the root system of the plant in the side row. After washing and chopping in the laboratory, 1-g root samples were used to quantify number of galls and egg masses, and to extract eggs with NaOCl. Another 1-g root sample was used for extraction of juvenile and adult nematodes with pectinase (25) for year 1A or for staining (2) for year 1B. Only swollen juvenile and adult nematodes were counted.

For determinations of the proportion of each species in the mixtures, roots from mixed-population plots were used to collect 20 egg masses for single-egg-mass bioassay on watermelon, and 20 females for species identification by esterase phenotypes (6). Bioassay of egg masses involved the placement of a single egg mass on the root of a single 5-day-old watermelon seedling planted in 1:1 mixture of steam sterilized sand and field soil (loamy sand) in a 7.5-cm-d pot. The pot was placed in an empty 10-cm-d pot to prevent contamination from surrounding plants. Assay plants were maintained in a greenhouse for 6 weeks. The root systems were then examined for the presence of galls, which indicated that the egg mass was MA1. The proportion of each nematode species was based on 20 plants.

At midseason, crop growth was subjectively rated using a 0–10 scale, based on

both plant vigor and leaf color (0 = dead; 10 = normal growth). At harvest, root systems and pods were rated for gall and necrosis indices (0–100% area galled or necrotic per root system or pod) (15). Root-nodule indices (1–10) also were subjectively made for each root system (1 = no nodule, 10 = heavy nodulated). Total pod yield per microplot was determined by dry weight.

Statistical analysis: To equalize variance, all nematode data were transformed to $\log_{10}(X + 1)$ before analysis. Analysis of variance (ANOVA) was performed for nematode counts, soil bioassay, and first-year crop-damage data. The HSD (Tukey's W; Honestly Significant Difference) was used for multiple comparisons of means. Correlation analysis was used to relate nematode infection and reproduction data for the first year, and to relate nematode population density at preplant (Pi) or midseason (Pm) of the second and third years with crop-damage data of each respective year.

Results

Nematode infection and reproduction: Root infection by nematodes was examined in the first year at midseason (both years 1A and 1B) and the time of normal harvest (year 1A only). Infection was determined by total parasitic forms of nematode (swollen juveniles or JP, and adults) in 1 g of roots. The number of nematodes released from roots by pectinase extraction was less than half of actual number assessed in stained roots. Peanut genotype and nematode treatment × peanut genotype interaction effects for nematode infection were detected at midseason only. The nematode × genotype effect was not evident in the repeated test (year 1B), and no genotype evaluated was resistant to nematode infection.

At midseason, infection levels of MA1 and of mixed populations were similar (200–300/g root), and these were greater than those of MH, except on NC 6 and NC Ac 18016, on which MA1 and MH had similar infection capacities in year 1A (Fig. 1A). Half-mixture and full-mixture populations had similar infection levels. At harvest, relative to MH or MH + MA1, MA1 had increased nematode numbers in roots (up to 1,000/g root), except on peanut NC

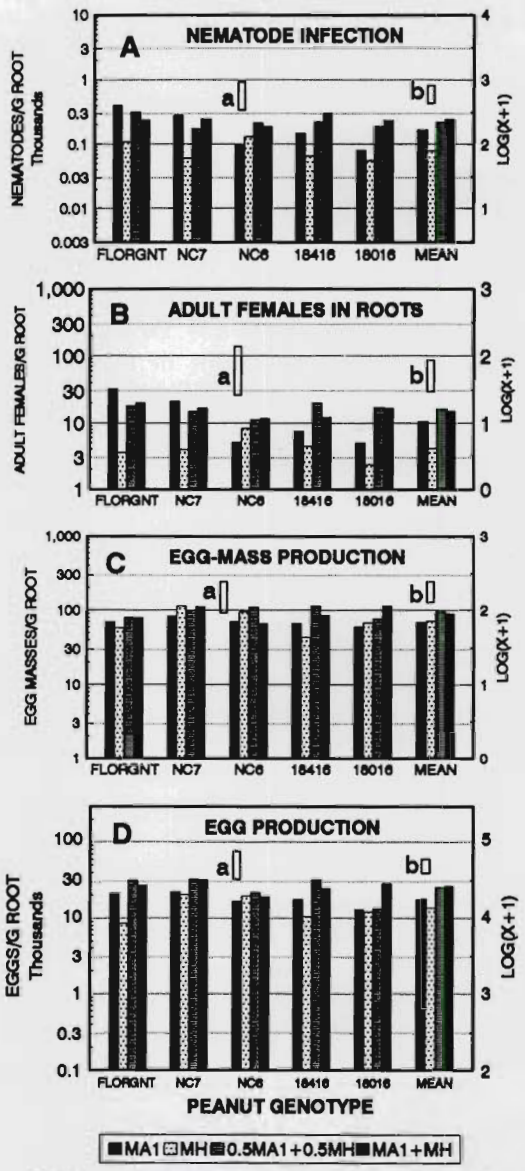

FIG. 1. A) Effects of peanut genotype on infection (total nematodes per g root). B) Female development (females per g root). C) Egg-mass production. D) Egg production of single or mixed populations of *Meloidogyne arenaria* race 1 (MA1) and *M. hapla* (MH) in microplots at midseason of the first year (year 1A, 1990). a, b represent HSD ($P = 0.05$) significant differences for mean comparison of nematode treatments within genotype and of nematode means, respectively.

Ac 18416, which had a low level of MA1 similar to that of MH (data not included). On other genotypes, MA1 and mixed populations had similar nematode numbers in roots.

Numbers of females of all populations at midseason were nearly proportional to infection levels (Fig. 1B). However, this was not true for the harvest sampling, at which time female numbers for MA1 and MH ranged from 10 to >50/g root, and were similar on all peanut genotypes. According to identification of esterase phenotype of 20 females from the full-mixture population at harvest of year 1A and from both mixed populations at 6 weeks before harvest of year 1B, the majority (89–100%) of females in roots was MA1 on all peanut genotypes (data not included).

Reproduction was measured by numbers of egg masses and eggs per gram of roots at midseason and harvest time of the first year, Numbers of egg masses also represented number of egg-laying females. At midseason, all nematode populations had similar numbers of egg masses on most peanut genotypes (except the slightly low egg-mass numbers of MH on NC Ac 18416) for both years 1A and 1B (Fig. 1C; data for year 1B not included). Egg production of MH alone was less than that of other populations on Florigiant and NC Ac 18416 for year 1A (Fig. 1D), and on NC 6 and NC Ac 18416 for year 1B. MA1 and both mixed populations had similar egg production potentials. At harvest, egg-mass production values of most populations were still similar to those at midseason, except that the values of MA1 and the mixtures on Florigiant and NC 7 had slightly decreased (data not included). However, no agronomically meaningful differences were observed among nematodes or among genotypes for egg mass or egg production.

Bioassays of 20 egg masses in the mixed populations showed that proportions of egg-laying females of MA1 to MH varied significantly (from 48–73% MA), with peanut genotypes at midseason but not at harvest (data not included). No difference between half- and full-mixture infestations was detected. At midseason the majority (60%) of egg-laying females in roots of Florigiant, NC 7, and NC Ac 18016 was MA1. On NC 6 and NC Ac 18416 egg-laying females of MA1 were about half for year 1A, and were slightly less than half for year 1B. At harvest (data for year 1A only), the majority (63%) of egg-laying females in the mixtures on most peanut genotypes was MA1. On NC 7 the proportion of MA1 was reduced to about half. On NC Ac 18416 the proportion of MA1 increased to more than half (70%).

Nematode population dynamics in soil: At midseason sampling of year 1A, only the numbers of second-stage juveniles (J2) were available to represent population densities in soil. For the later samplings, both J2 and eggs were included to represent the nematode densities. Few, nematode × peanut genotype interactions were detected, so only nematode means are presented (Table 1, Fig. 2). In the first year, reproduction factors (RF = Pf/Pi) of all populations among nematode treatments were not different (Table 1). However, in the repeat test (year 1B, 1992), the full-mixture population had the lowest RF. In mixed infestations (according to bioassay of microplot soil in greenhouse) MA1 predominated over MH on all genotypes at both mid-season and harvest. The mixed nematode populations induced as many galls on MH-resistant watermelon roots as did MA1 (data not included).

After harvest of the first year (HV 90), all population densities in soil declined (Fig. 2). In early spring (SP 91), total nematode numbers (J2 + eggs) of all populations were not different. Nevertheless, MA1 had the lowest survival rate (Pi of year 2/Pf of year 1) (Table 1). At late mid-season (110 days after planting) of the second year (MS 91), MH had the greatest population densities in soil on all peanut genotypes (resulting from the highest levels of eggs [Fig. 2]).

At the end of the growing season (HV 91), all populations had declined. The greatest reduction in overall populations

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TABLE 1. Reproduction factors (RF = Pf/Pi) and survival rates (Pi of current year/Pf of previous year) of single or mixed populations of *Meloidogyne arenaria* race 1 (MA1) and *M. hapla* (MH) in each season of different peanut genotypes in microplots (only nematode means given).

Nematode population treatment	Reproduction factor (RF)				Survival ratio	
	Year 1A (1990)	Year 1B (1992)	Year 2 (1991)	Year 3 (1992)	After year 1A (Pi year 2/Pf year 1A)	After year 2 (Pi year 3/Pf year 2)
MA1	105.7	60.7	2.9	9.0	0.19	0.34
MH	104.5	54.2	1.0	9.0	0.38	0.17
0.5 MA1 + 0.5 MH	101.4	64.9	1.5	8.2	0.29	0.21
MA1 + MH	75.0	24.1	0.3	21.0	0.32	0.31
HSD $P = 0.05$	NS	25.5	2.6	8.2	0.15	NS

All data are means of five genotypes with six replicates each, except five replicates for year 1B (repeat experiment of first year, 1990).

Analyses were based on $\text{Log}_{10}(X + 1)$ transformed data (genotypes were as follows: Florigiant, NC6, NC7, NC Ac 18416, and NC Ac 18016).

appeared with MH. Most infestations had final population densities under maintenance levels. The reproduction factors of the full-mixture population were less than those of other infestations, on most genotypes (Table 1).

According to bioassays of microplot soil using watermelon in a greenhouse and esterase phenotype identification, MA1 dominated over MH in mixed infestations on all genotypes at both midseason and harvest. The degree of dominance of MA1 on the two mixed populations was not different (data not included).

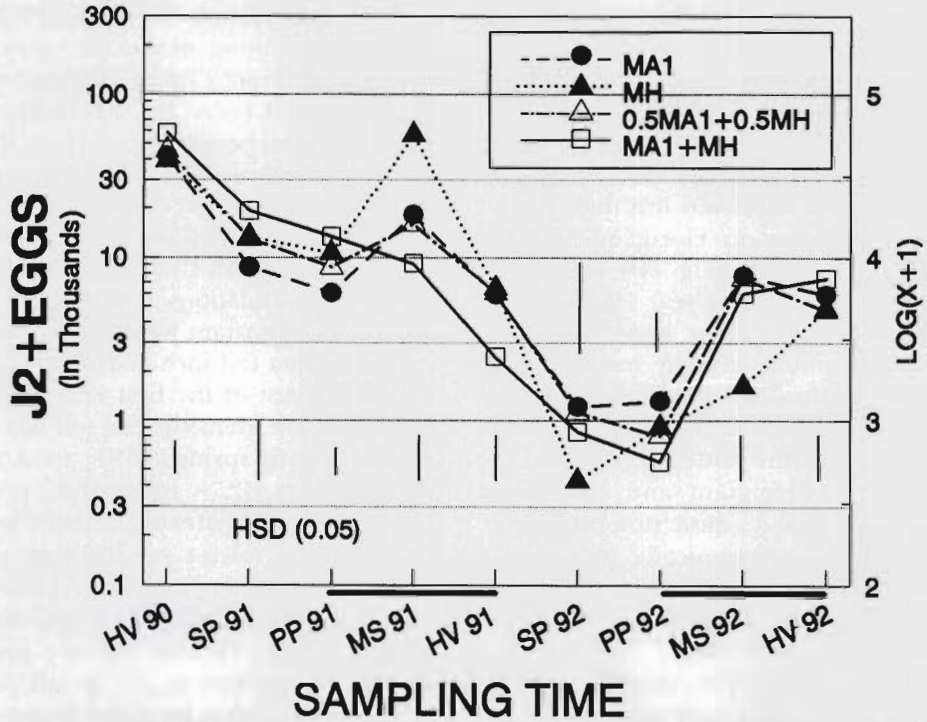

FIG. 2. General population dynamics of single or mixed populations of *Meloidogyne arenaria* race 1 (MA1) and *M. hapla* (MH) from harvest 1990 to harvest 1992 in microplots planted to different peanut genotypes (means per 500 cm^3 of soil for five genotypes). Bars represent HSD ($P = 0.05$) significant differences for mean comparison of nematode treatments across genotype at different sampling time. HV = harvest, SP = spring, PP = preplanting, MS = midseason.

After the second season (1991), all populations continued to decline (Fig. 2). In early spring (SP 92), numbers in soil among all populations were not different. Very low population densities of MH were present on most genotypes at this time, but the population showed an increase at preplanting (PP 92). At preplanting, all populations had similar total densities, with MA1 + MH being the lowest. During crop-free periods, egg numbers of all populations were at a low to almost undetectable level. Survival rates (Pi of year 3/Pf of year 2) of all nematode populations from most genotypes did not differ, but MA1 tended to have greater survival rate than did MH (Table 1).

In 1992, all nematode populations increased sharply in the soil after planting (Fig. 2). MA1 and half-mixture populations peaked at midseason (MS 92), whereas the lower MH and full-mixture populations were still increasing after midseason. Numbers of eggs in soil of all populations were not different. At harvest of the third year (HV 92), the total numbers of all populations were similar, except on peanut NC Ac 18416, on which MH had the lowest density (resulted from slow multiplication; data not included). Final numbers of all populations were above the maintenance level. The full-mixture population had the greatest reproduction factor (Table 1). According to bioassays of microplot soil for the third year, MA1 still dominated over MH in mixed infestations, as was true in the first 2 years (data not included).

Crop damage: With the same inoculum densities in the first year, MA1 and half-mixture populations induced similar damage on peanut, and both induced greater damage than did MH alone (Table 2). Damage caused by full-mixture population was similar to that caused by half-mixture infection. At midseason of the first year (year 1A, 1990), plant growth (vigor and color) in all nematode treatments was similar, and these were only slightly different from the control plants. In the repeat experiment (year 1B), crop growth (growth index) in the MH treatment was better than that of MA1 and full-mixture nematode treatments, but was still lower than that in control plots (data not included).

At harvest, root and pod-galling indices induced by MA1 and mixed populations were greater than those induced by MH for all genotypes (Table 2). The two mixed populations caused a similar degree of galling. The root and pod necrosis induced by MA1 was similar to MH in the 1990 test (year 1A) (Table 2), but produced more necrosis than MH for year 1B (except on NC 6) (data not included). Mixed populations also induced more necrosis on roots and pods than did MH. Yield suppression caused by MH was less severe than that induced by MA1 and full-mixture population. All genotypes responded to MH similarly in the 1990 experiment. In the repeat test (year 1B), Florigiant was more sensitive to MH than other genotypes, and cultivar NC 6 had less damage caused by MA1 and mixed populations than did other genotypes (data not included).

In the second year, severe crop damage was obvious before midseason. Many plants died before harvest. Crop growth, root nodulation, and yield were negatively correlated with Pi, whereas root and pod damage were positively correlated with Pi (data not shown). *Meloidogyne hapla* caused less damage to roots and pods than did other infections (Table 2).

In the third year, crop damage was obvious by midseason. Relationships between crop response parameters and Pi or Pm were similar to those in the second year. However, correlation coefficients for crop responses with Pm were greater than with Pi. *Meloidogyne hapla* still produced less damage to peanut than did other populations (data not included).

Discussion

By definition, crop resistance to nematodes is based on reproduction of the parasite rather than penetration of roots (3). Factors affecting the development of the juveniles following penetration, however,

TABLE 2. Root and pod damage of peanut by single or mixed populations of *Meloidogyne arenaria* race 1 (MA1) and *M. hapla* (MH) in microplots at harvest.†

Nematode population	Root-gall indices (0–100)†	Root-necrosis indices (0–100)†	Pod-gall indices (0–100)†	Pod-necrosis indices (0–100)†	Dry-pod yield (g)
		1990			
MA1	59	27	57	16	—‡
MH	36	20	31	19	—
0.5 MA1 + 0.5 MH	69	35	68	24	—
MA1 + MH	73	41	66	32	—
Control	0	9	0	7	—
HSD (P = 0.05)	9	10	13	18	
		1991			
MA1	85	79	87	58	62
MH	29	22	20	13	99
0.5 MA1 + 0.5 MH	82	82	87	58	31
MA1 + MH	87	77	76	34	18
Control	0	7	0	5	464
HSD (P = 0.05)	10	11	NA‡	NA	36
		1992			
MA1	79	38	50	33	43
MH	26	19	9	12	102
0.5 MA1 + 0.5 MH	79	38	58	27	19
MA1 + MH	82	32	57	22	36
Control	0	10	0	8	226
HSD (P = 0.05)	7	9	17	14	26

Data are means of five peanut genotypes; Florigiant, NC6, NC7, NC Ac 18416, and NC Ac 18016 (six replicates/genotypes).
† 0 = no gall or necrosis, 100 = 100% root- or pod-surface galled or necrotic per root system or plant.
‡ NA = No statistical comparison due to missing values (severe damage resulted in no pods).

may be involved in this type of resistance (8). Early penetration into roots of resistant or unsuitable hosts by *Meloidogyne* spp. may be similar to those of suitable hosts (8,9). Failure of juveniles to further develop into females (producing eggs) had been demonstrated as a general resistance mechanism in several wild *Arachis* spp. (17,23). Results of the present study also indicated that infection incidence was not related to reproductive efficiency. For example, MH effected lower infection than did MA1 single or mixed populations in most cases, but all nematodes had similar reproduction potentials.

According to a preliminary greenhouse evaluation of host suitability of peanut cultivars (21), based on root damage and nematode reproduction, Florigiant is hypersusceptible (high damage, low reproduction) to MA1 but resistant (low damage, low reproduction) to MH. NC 7 is resistant to MA1 but hypersusceptible to MH; and NC 6 is resistant to both nematode species. The present microplot study showed that these three peanut cultivars, together with two breeding lines, NC Ac 18416 and NC Ac 18016, in fact, were susceptible to both nematode species and their combinations. The earlier greenhouse tests (21), involving inoculations of seedlings with 5,000 eggs in 10-cm pots and harvests after 60 days, may have provided inadequate time for resistance evaluations. In our study, all nematode populations had similar reproduction capacities on all five peanut genotypes, but MH induced less damage than did other populations. Among five genotypes, however, NC 6 seemed to be more tolerant (same reproduction, less damage) to the two nematode species, and their combinations, than other genotypes. The similarity in host suitability of these five genotypes to MA1 and MH resulted in little influence on the interaction between the two nematode species. The divergence from the earlier greenhouse work reported by Sasser et al. (21) is likely related to the different test conditions. Although greenhouse results usually

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correlate with those from the field, the latter generally place more realistic stress on plants than do the former, and peanut generally requires more time for root-knot nematode population increases than many other hosts.

The greater proportion of MA1 females over MH (detected by esterase phenotypes) in the mixed populations indicates that MA1 was more competitive than MH in infection and reproduction processes on peanut after midseason. The predominance of MA1 in roots was also confirmed by soil bioassay. Because MA1 predominated over MH in the mixed infestations in soil, root infection of the mixed populations could be effected mostly by MA1 (which had greater infection potential than did MH).

The mechanism of competition between MA1 and MH is unknown. Kinloch and Allen (14) observed that the decreased competitiveness of *M. hapla* when combined with *M. javanica* was probably due to the restriction of invasion sites (i.e., active meristem) for *M. hapla,* whereas *M. javanica* can penetrate galled tissue as well as root tips. Rapid necrosis of root tips induced by the more competitive species could also limit invasion sites available for *M. hapla* juveniles, as found in tobacco (12). These mechanisms may be involved in infection competition between MA1 and MH in the present study, resulting in the predominance of the former nematode.

Despite having lower infection potential than MA1 and the mixture, MH as a single population developed numbers of egg-laying females (estimated from egg-mass numbers) that were similar to MA1, but depending on the infection load, fewer females may produce more eggs each (less competition for food), regardless of species. These results suggest that juveniles of MH developed into reproductive females more efficiently than did those of MA1 and the mixed populations, and thereby reached a reproductive potential similar to the others. Although the single MH population was almost as prolific as MA1, when it was mixed with MA1, MH was suppressed by the latter.

Meloidogyne hapla has a lower optimum temperature for reproduction than MA1 (24). The low egg production of MH on some peanut genotypes at midseason in the 1992 repeat experiment (year 1B) might be, in part, due to unfavorably warm soil temperature. Near the end of the season the temperature was cooler, and reproduction increased, resulting in a RF similar to that of MA1 and MA1-dominant populations. Temperature could have affected egg mass size rather than number of egg masses (or egg-laying females) because all populations produced similar numbers of egg masses. Plant genotype also could have influenced egg mass size as observed for *M. incognita* in asparagus (7) and for *M. javanica* in carrot (10).

In the mixed populations on most peanut genotypes, the majority of egg-laying females was MA1 (according to single-egg-mass assay). This, in part, resulted from a greater infection potential of MA1 in MA1-dominant mixture populations. In the 1992 repeat test (year 1B), proportions of MA1/MH in mixed populations were highly variable. However, both tests had a similar tendency in that the MA/MH ratio on NC 6 and NC Ac 18416 was smaller than that on the other three genotypes. Similar infection and reproduction potentials of the half- and full-mixture populations suggest that the antagonistic competition in the full-mixture might be stronger than in the half-mixture, or the half-mixture was approaching the carrying capacity of peanut, with no additional infections in the full mixture.

In the first year, with low initial inoculum levels, crop growth was much better than in successive years, and no plants died before harvest. Nematodes had sufficient food resources to reproduce until plant harvest. In contrast, at preplant time of the second year the numbers of each population surviving from winter were high (more than 10-fold of first year Pi); subsequently, they caused severe damage before midseason, especially to Florigiant and with the full-mixture population. The severe damage to roots by high-density MA1

and MA1-dominant (mixed) populations resulted in a population decline before midseason sampling. These results indicate that midseason densities cannot be accurately used to reflect final crop yield or damage if Pi densities were high. When Pi densities were low, as in the third year, midseason densities may reflect final crop damage.

Meloidogyne hapla had been reported to be the most damaging species of root-knot nematode of peanut in North Carolina (1). Recently, the importance of *M. arenaria* race 1 has been increasing in this state, and more infestations in peanut fields with severe crop damage have been reported (4,22). *Meloidogyne arenaria* race 1 has a high reproductive potential and winter-survival rate, and causes more damage to peanut than does *M. hapla* in more Southern states (15). In mixed infestations, *M. arenaria* race 1 is more competitive than *M. hapla* on peanut. Thus, *M. arenaria* race 1 may become dominant and play an increasingly important role in peanut production in the northern peanut belt. Higher levels of resistance to both nematodes than that in the five genotypes described herein is needed for more effective management of these pathogens.

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